

ORIENTATION AND CURRENT-INDUCED FLOW IN THE STALKED ASCIDIAN *STYELA MONTEREYENSIS*

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Virtually all sessile suspension feeders rely on ambient water movement to renew their food supplies and to carry away waste products and depleted water. In addition, species in many taxa have developed hydrodynamic mechanisms for exploiting the energy in the velocity gradient between the substratum and the moving water. For instance, exogenous currents induce flow through tubes, burrows, or internal chambers, and across external food-collecting surfaces (Vogel, 1978). Where currents are predictably unidirectional or bidirectional, colonial organisms frequently exhibit a permanent orientation which maximizes exposure to current (Wainwright and Dillon, 1969; Grigg, 1972; Meyer, 1973). In areas with turbulent water or currents of unpredictable direction, orientation-independent mechanisms are common (Warner, 1977). These are exemplified by animals with irregular or radial forms, such as sponges (Vogel, 1974) and some crinoids (Meyer, 1973). While barnacles (Crisp and Stubbings, 1957) and brachiopods (La Barbara, 1977) reorient actively when the current direction changes, certain sea anemones (Koehl, 1976), conical stalked hydroids, and erect bryozoans allow currents to orient them passively (Warner, 1977).

Monniot (1967) has reported that the subtidal ascidian *Microcosmos vulgaris* normally orients its siphons up-current, but is capable of actively reorienting when suspended material becomes too dense. Surprisingly, evidence for induced flow has been presented for only one ascidian species, *Styela plicata* (Bretz, 1972).

Styela montereyensis is a common stolidobranch ascidian in the Northeast Pacific. Johnson and Abbott (1972) have redescribed the species clearly, calling attention to morphological variation within and among local populations. The animal is anchored by an irregular tunic holdfast and held more or less erect in the water by a long stalk. Although both siphons are inserted anteriorly as in most ascidians, the larger incurrent siphon is recurved to point either posteriorly or ventrally. The entire body appears longitudinally plicated due to alternating thick and thin tunic areas.

Preliminary diving observations indicated that the flexible stalk of *Styela* allows ambient currents to reorient the animal passively, facilitating induced flow. The mechanism by which this occurs operates regardless of the direction from which the current comes. This feature is appropriate since *Styela* characteristically occupies shallow water where the surge oscillates, sometimes in unpredictable directions, every few seconds.

In this paper, we document current-induced flow and describe aspects of orientation, morphological variation, habitat utilization, and larval habitat selection related to the use of currents by *Styela*.

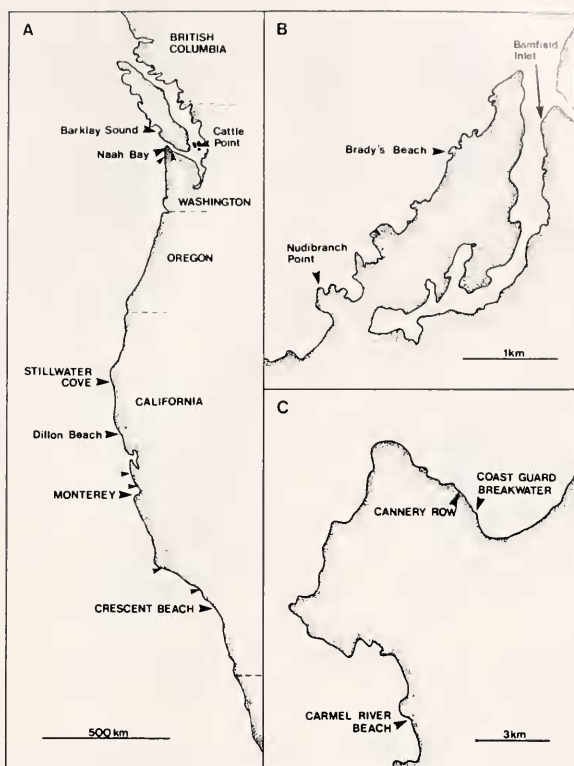


FIGURE 1. A) Known geographical range of *Styela montereyensis* on the Pacific Coast of North America, showing main study areas. Subtidal sites are capitalized. Unlabelled arrows indicate sites where *Styela* was not found. B) Mills Peninsula in Barkley Sound, British Columbia, showing 2 protected outer coast sites and a nearby protected site. C) Study sites on the Monterey Peninsula, California.

MATERIALS AND METHODS

We collected or observed *Styela montereyensis* at 11 sites from southern California to Vancouver Island (Fig. 1), thereby covering the species' known geographical range (Van Name, 1945). Although *Styela* characteristically occurs in areas of vigorous water movement (Fay and Vallee, 1979), its occasional appearance in quiet bays allowed us to compare morphology of specimens collected from a variety of current regimens. We made no quantitative measurements of current velocities, so our designations of sites as "open coast," "protected outer coast," or "protected bay" are based on subjective evaluation of local geography, surf, and fauna, following the criteria of Ricketts and Calvin (1962).

The nature of the substratum, approximate incline of the surface of attachment, orientation of the attachment surface relative to the direction of the prevailing surf or surge, depth or tide level, and approximate dimensions of the substratum were recorded for each individual we encountered while diving or collecting intertidally. Relative stalk length of each animal was determined in the laboratory by measuring the compression-resistant portion of the stalk and expressing this value as a fraction of the total body length exclusive of expanded siphons.

Living animals were transported in cold seawater (on ice, where necessary) to aquaria at Hopkins Marine Station, California; Friday Harbor Laboratories, Washington State; Bamfield Marine Station, British Columbia; or Brigham Young University, Utah. Larval cultures and live adults were maintained at 8°–14°C, depending on the season and the seawater system used.

At Neah Bay, Washington, we recorded the permanent orientations of ascidians relative to the horizontal. This was done at low tide by loosely holding each animal perpendicular to the piling, viewing it from the anterior end, and drawing an arrow on a slate to represent the direction the incurrent siphon pointed. The angles of the arrows were later measured using a protactor and placed in a "rose diagram" frequency distribution which was compared with a circular-normal distribution using chi-square (Batschelet, 1965).

Internal flow rates were estimated in a running seawater flume in which current velocity could be varied by regulating incoming water volume and the size of the outlet channel. Current speed in the tank was measured by repeatedly timing the passage of fluorescein dye along a 1 m course. Each animal was tied by its holdfast to a small weight in the flume, with the animal's incurrent siphon directed upstream. When the animal acclimated, about 1 ml of red food coloring (F.D.C. red #9,40) in seawater solution was introduced into the incurrent siphon with a pipette. A hand-held stop watch was used to measure the time elapsed before reappearance of the dye at the excurrent siphon. Twenty trials were made with each animal at each of several current speeds. The ascidians showed no adverse reaction to the dye, though they closed up in response to low concentrations of fluorescein or rhodamine.

To assess the possible influence of stalk flexibility on feeding, the rates of ingestion by animals free to sway with the currents were compared with those of animals restrained upright. Specimens of intermediate size (12 ± 2 cm) were collected from the Cannery Row site and held in clean seawater aquaria for 48 hr to clear food from their guts. Animals were paired by size (± 0.1 g, dry weight) and one of each pair randomly designated as the experimental animal. Each control animal was wired by its holdfast to the surface of a commercial structural brick, so that it could move freely. Each experimental animal was either anchored within a hole in the brick or caged above the brick in a narrow tube of 0.5 cm plastic mesh (Fig. 2). By restraining the experimental animals at two different vertical levels in this fashion, we hoped to control for boundary-layer and turbulence effects; some animals would feed at the vertical level of a flexed control animal while others would feed at the level of an erect control animal. The bricks with tunicates attached were placed in Monterey Bay at 4 m depth and left for 24 hr. They were then retrieved and brought into the laboratory, where the ascidians were removed and isolated in separate bowls of seawater. All feces expelled over the subsequent 24 hr were collected on pre-tared filter papers and washed with distilled water. Filter papers and animals were oven dried at 50°C and weighed on an analytical balance sensitive to 0.001 g.

Tadpole larvae were reared from spawned gametes or gametes removed by dissection. Responses of the settling larvae to light and gravity were assessed by examining the settling distributions of larvae in 16-ml-capacity molded-polystyrene petri dishes completely filled with water and covered on one side with black plastic tape (Young and Braithwaite, 1980). The dishes were cooled in a shallow seawater table under incandescent light at an intensity of 1500 lx.

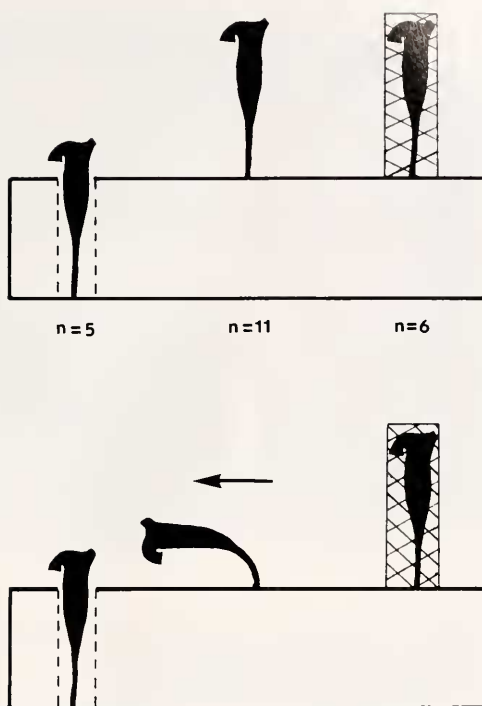


FIGURE 2. Schematic drawing of field feeding experiment, showing positioning of restrained and control animals in calm water (top) and current (bottom).

In a second experiment, larvae were placed in a circular channel, 5.75 cm wide and 3 cm deep, created by positioning a glass stacking dish in the center of a large shallow battery jar, half darkened with opaque black plastic. Twin air jets at opposite sides of the dish moved water and larvae around the channel at an average speed of 3 cm/sec. The tadpoles, slowly moving between the light and dark sides of the dish, were thus given the opportunity of settling anywhere along two continuous light-dark gradients, simulating conditions they might encounter in the field, where currents move them over illuminated and shaded portions of the substratum. After all animals settled, the distribution of zooids was plotted to the same scale on a large piece of paper. A protractor was used to divide the circular plot into 10° sectors. The number of animals in each sector was recorded, and each sector was paired with each opposite sector for a two-way analysis of variance in which the within-treatment variance tested the position of the sector pair relative to the air jets and the between-treatment variance tested light versus dark.

In a final series of experiments, groups of larvae were maintained in bowls of filtered seawater in continuous light or continuous dark. The dishes were monitored every few hours to assess the difference in settling times for larvae reared under these radically different lighting conditions. Yamaguchi (1970) and Crisp and Ghobashy (1971), working with other ascidian species, established precedent for this experimental design.

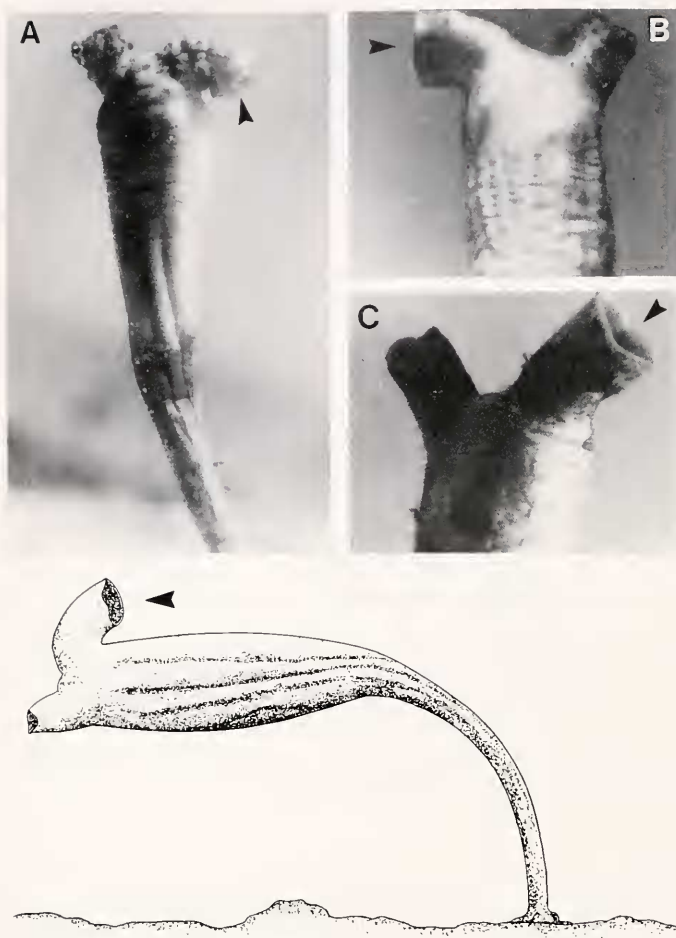


FIGURE 3. (Top.) Typical siphon inclinations of *Styela montereyensis* collected from the open coast (A) and protected bays (B, C). Arrows indicate incurrent siphon apertures.

FIGURE 4. (Bottom.) Current-facilitated orientation in *Styela montereyensis*.

RESULTS

Phenotypic plasticity

Two major morphological characteristics, incurrent siphon curvature and relative stalk length, varied among animals inhabiting different current regimes. By observing numerous animals in laboratory aquaria over periods of up to 2 months, we concluded that each consistently points its expanded incurrent siphon in a specific direction relative to its own longitudinal axis. The curvature which determines this direction apparently results from differential growth in the walls of the siphon. Specimens collected from all sites on the open coast or protected outer coast, either intertidally or subtidally, characteristically had siphons curved nearly 180° from the anterior point of insertion. The aperture was thus directed posteriorly. With few exceptions, animals collected from the two protected sites displayed ventrally-directed incurrent siphons (Fig. 3), as did some animals collected from deeper than 12 m in Monterey Bay.

TABLE I

Relative stalk lengths of *Styela montereyensis* at several sites (ranked subjectively by exposure). Variation among group means significant at $P < 0.001$ (Cattle Point site not included in analysis because of small sample size). OC: open coast; PC: protected outer coast; PB: protected bay.

Site	Exposure	N	Mean relative stalk length	Standard deviation
Stillwater Cove	OC	15	0.659	0.054
Barkley Sound	PC	14	0.655	0.066
Crescent Beach	PC	5	0.541	0.045
Breakwater	PC	50	0.572	0.066
Dillon Beach	PC	13	0.545	0.054
Bamfield Inlet	PB	9	0.470	0.031
Neah Bay	PB	80	0.388	0.061
Cattle Point	PB	2	0.461	0.033

Table I gives relative stalk lengths of animals from each site. Stalks are significantly longer in more exposed habitats, with the between-group variance component being significant at $P < 0.001$ by one-way analysis of variance.

Orientation and induced flow

Different orientation mechanisms are employed by *Styela* in habitats with different current regimes. In subtidal habitats with strong oscillating surge, *Styela* orients as follows: Each wave that passes onshore bends the flexible stalk far enough to align the longitudinal axis of the animal with the current. The subsequent backsurge instantly flips the animal 180° aligning it once again (Fig. 4). In either position, the recurved incurrent siphon points directly upcurrent. If the

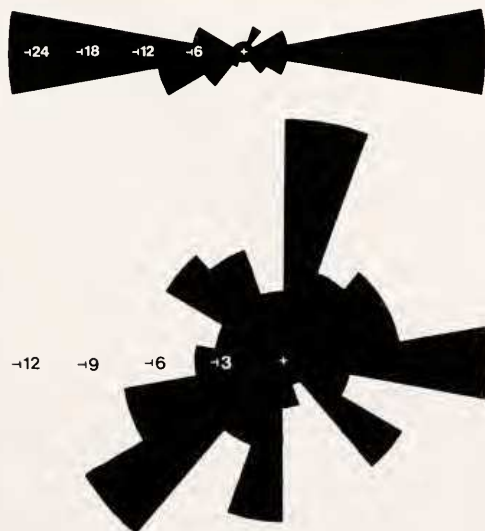


FIGURE 5. (Top.) Orientations of 95 *Styela* adults on vertical pilings in Neah Bay, as percentage of animals with incurrent siphon orientation falling within each 20° sector. Orientation is non-random ($P < 0.001$) by chi-square.

FIGURE 6. (Bottom.) Orientations of 95 juvenile *Styela* (< 3 cm long) on pilings at Neah Bay, shown as percentages as in Figure 5. Orientation is random ($P > 0.05$).

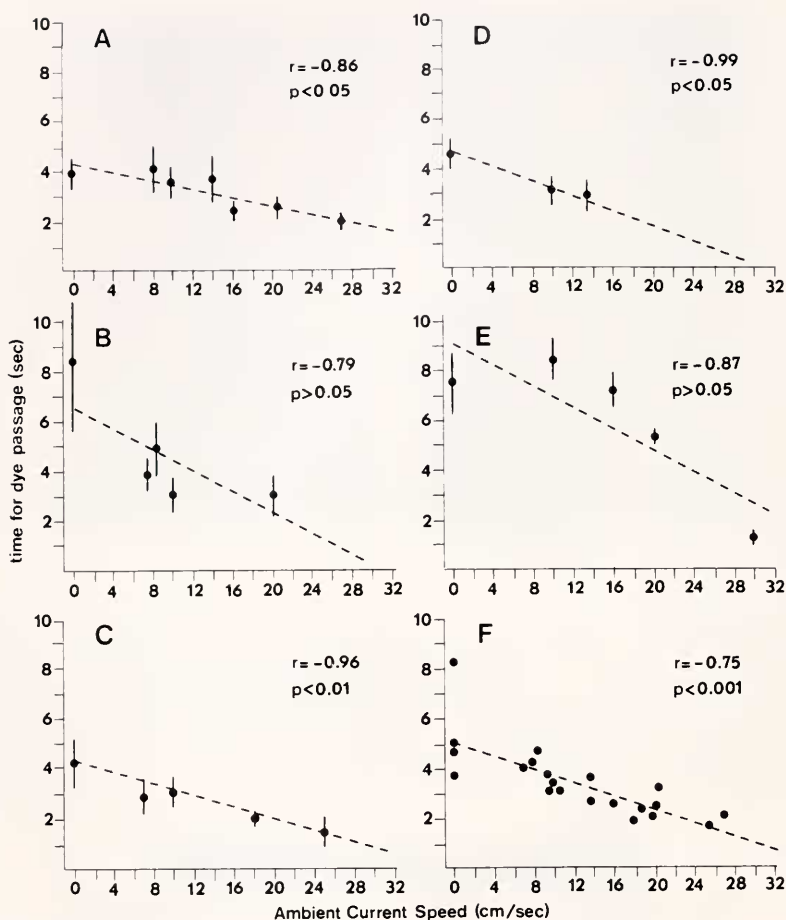


FIGURE 7. Relationship between current speed and internal filtering rate (measured by the time elapsed while dye passed from the incurrent to the excurrent siphon) in *Styela montereyensis*. Each point represents mean of 20 trials, shown with 95% confidence interval. A-D) 11 to 12 cm long animals. E) 15 cm long animal. F) Pooled data from A-D (shown without confidence intervals for clarity).

animal is anchored without nearby obstructions, orientation is effective regardless of the direction from which the current comes.

In quiet bays, the surge is seldom enough to sway the short-stalked animals. Individuals in Neah Bay attached to wooden pilings and floats display a permanent orientation. A significant majority of animals longer than 3 cm have their mid-sagittal planes aligned parallel with the surface of the water (Fig. 5). Thus, the ventrally-directed incurrent siphons of most animals are pointed upcurrent (into either the surge or the backsurge) 50% of the time. Very small individuals are pointed randomly (Fig. 6), so the adult orientation apparently results from rotational growth rather than larval behavior or reorientation shortly after settling. Further indication of this is that the longitudinal furrows of Neah Bay specimens often spiral in the stalk region, while those of subtidal outer coast specimens most frequently run straight from the holdfast to the anterior end.

TABLE II

Fecal production by restrained and unrestrained Styela in subtidal feeding experiment.

Restrictive treatment	Animal dry weight (g):		Fecal weight (g)/Body weight (g):	
	Unrestrained	Restrained	Unrestrained	Restrained
hole	0.192	0.186	0.052	0.037
hole	0.408	0.286	0.046	0.017
hole	0.345	0.258	0.029	0.012
hole	0.332	0.256	0.057	0.004
hole	0.194	0.199	0.072	0.015
cage	0.175	0.167	0.068	0.036
cage	0.150	0.151	0.186	0.033
cage	0.214	0.229	0.168	0.030
cage	0.901	0.855	0.026	0.019
cage	0.767	0.741	0.027	0.013
cage	0.755	0.689	0.039	0.013

In laboratory flume experiments utilizing animals from Monterey Bay, flow through the branchial basket and atrium increased at higher current speeds. Furthermore, in most cases the relationship between external current speed and internal flow was significantly linear (Fig. 7). We augmented the number of points available for regression analysis by pooling data from all animals 11–12 cm long. Despite obvious behavioral differences between individuals, the points conformed to a linear model at the 0.001 level of significance. The maximum current speed tested with each animal was determined by the animal itself. Beyond a certain point, ranging from 14 to 30 cm/sec, each animal contracted its siphons and stopped filtering.

In ascidians, correlation between internal and external flow is not necessarily indicative of enhanced feeding, for two reasons. First, ascidians may be capable of increasing the activity of their lateral cilia when detecting current. Second, they are capable of filtering without actually feeding, by interrupting the secretion of endostyle mucus (MacGinitie, 1939). Our field experiment, in which ingestion (measured by fecal production) was compared in restrained and unrestrained animals, was designed to meet both of these potential objections.

All animals in the field experiments survived their respective treatments without apparent abrasion or other damage, and all animals fed while in the field. Within each pair of animals, the restrained animal always consumed less food (Table II). There was no consistent difference between the two restrictive treatments, so data from all pairs were pooled. Paired one-way analysis of variance revealed a significant difference ($P < 0.01$) between means of the restricted and control groups. Assuming all animals move food through their guts at a constant rate and that this rate is more or less independent of the volume of food ingested, we conclude that induced flow actually enhances feeding in the field. C. K. Goddard (University of New South Wales, personal communication, 1978), in using markers to trace the passage of food through the guts of other stolidobranch species, has shown both of the above assumptions to be true.

Habitat utilization

Styela montereyensis is found on hard substrata from the mid-intertidal to at least 15 m depth. Although the overwhelming majority of animals are attached to

TABLE III

Percentage of animals at each site free to sway horizontally in all directions, obstructed on one or more sides, or in surge channels.

Site	Intertidal (I) or subtidal (S)	No. man-dives or low tides	N	% Unobstructed within radius	% Obstructed within radius	% In surge channel
Breakwater	S	9	89	98.9	1.1	0.0
Cannery Row	S	4	29	100.0	0.0	0.0
Carmel River Beach	S	4	11	81.8	0.0	18.8
Stillwater Cove	S	3	21	66.7	0.0	33.5
Crescent Beach	S	3	9	0.0	100.0	0.0
Dillion Beach	I	3	14	0.0	21.4	78.6
Barkley Sound	I	3	13	23.1	23.1	53.8

large subtidal boulders or rock reefs, specimens of *Styela* are also found on a variety of other substrata including wooden pilings and floats, styrofoam floats, rubber tires, steel pipe, and cement. They occur as epizooites on the barnacles *Balanus nubilus* and *Balanus cariosus*, the mussel *Mytilus californianus*, the ascidians *Styela montereyensis* and *Pyura haustor*, and the algae *Cystocira osmundacea* and *Gigartina californica*. In addition, some specimens at the Monterey Breakwater site are found anchored in sand. These latter animals have unusually large and ramified holdfasts for securing themselves in soft sediment.

Since surge currents are generally horizontal (Bascom, 1964), we hypothesized that animals on vertical surfaces might be in danger of battering against their substratum when the surge approaches head-on. Field observations support this hypothesis. Table III compares the number of animals at each site that are free to sway in any horizontal direction within their own radius with animals not free to sway. A significant majority of animals occupy the unobstructed positions, which are nearly always on the upward-facing surfaces of rocks or reefs. Animals on vertical surfaces are usually in surge channels where there are physical constraints on the direction of water movement.

At Crescent Beach, an extensive survey failed to reveal any specimens except on a single face, angled about 45° to the horizontal. Although the absence of an opposing face in close proximity precludes our classifying this site as a surge channel, we note that the attachment surface is aligned perpendicular to the beach in a small bay where the surf approaches from a single direction.

In the rocky intertidal, most animals occur either in surge channels or on the back sides of boulders, where water passes around the rocks on the backwash, creating effective surge channels where *Styela* orients by swaying in the usual fashion.

Larval settling behavior

We obtained abundant spawned or dissected gametes during every month of the year except March, July, and October, when we made no attempts. Embryogenesis (fertilization to hatching) takes 2 days (at 8°C) and the larvae may delay metamorphosis up to 6 days. Planktonic life may therefore be as long as 8 days.

Styela tadpoles are not strongly photonegative at settling. In eight replicate polystyrene dishes with an average of 100 tadpoles per dish, there was no significant preference for light or dark ($P = 0.844$; Wilcoxon signed-rank test). We ran two light-dark choice experiments in which larvae drifted passively around the dish with air-driven currents, one with 2441 tadpoles from Neah Bay and one with 183

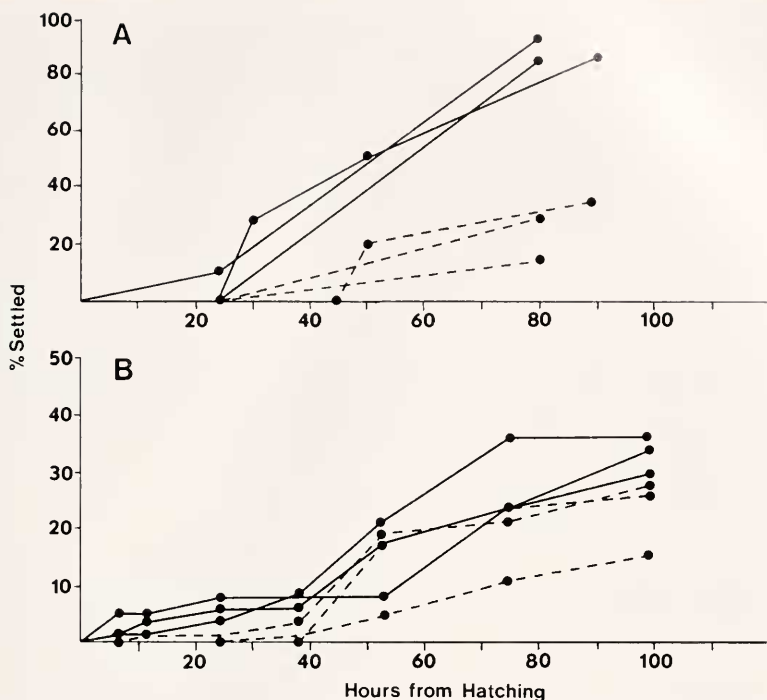


FIGURE 8. Settlement of *Styela montereyensis* larvae in complete darkness (dotted lines) and continuous light (solid lines). Each line represents a replicate run with 50 tadpoles. A) three experiments using tadpoles from Monterey Bay animals. B) three experiments using tadpoles from Neah Bay animals.

tadpoles from Monterey. The difference in settlement between light and dark was non-significant ($P < 0.5$, $P < 0.1$) by two-way analysis of variance, while the variance attributed to current effects was non-significant in the Neah Bay experiment ($P > 0.75$) and significant in the Monterey experiment ($P < 0.05$). This last difference is probably not due to a behavioral preference for a particular current regime; non-laminar flow in the dish apparently caused pooling in some regions, resulting in uneven settlement.

Styela larvae tend to be relatively lethargic, especially at the end of larval life when they generally rest on the bottom or drift passively rather than swim up in the water column. In the petri dish experiments, significantly more larvae settled on the bottoms of the dishes than on the undersides of the lids ($P = 0.008$; Wilcoxon signed-rank test). Ascidian species with more active tadpoles often show the opposite response in identical experiments (Young, unpublished data).

Both *Ciona intestinalis* (Yamaguchi, 1970) and *Diplosoma listerianum* (Crisp and Ghobashy, 1971) delay metamorphosis in continuous light. By contrast, *Styela montereyensis* tadpoles delay metamorphosis in continuous darkness (Fig. 8). This response is stronger in animals of the open coast than those of protected bays, but the reason for this difference is not known.

DISCUSSION

Among animals that utilize ambient currents for feeding, *Styela montereyensis* represents an extreme in adaptiveness. Its feeding mechanism is unusual in that

efficient induced flow depends on precise orientation in habitats where current direction oscillates on a scale of seconds. *Styela* uses the force of the surge not only to induce flow, but also to effect the orientation that makes this current utilization possible. Thus, foraging may require little energy beyond initial growth and normal body maintenance.

Vogel (1978) has outlined three transducing mechanisms for inducing flow in biological systems: dynamic force, the Bernoulli effect, and viscous entrainment. At least two of these apparently play some role in the feeding of *Styela*. When *Styela* is aligned with the current, water is pushed through the feeding apparatus primarily by dynamic force against the incurrent siphon, but this effect is probably reinforced by viscous entrainment in which some water is drawn out of the excurrent siphon. In Neah Bay animals, dynamic force and viscous entrainment aid filtering when water comes from one direction only. On the backsurge, viscous entrainment should theoretically draw some water out of the incurrent siphon. We hypothesize that the effect of this entrainment is minimal and does not significantly offset the advantage obtained by part-time orientation.

Current utilization is enhanced in different habitats by the phenotypic plasticity of the species. Both open-water and protected bay forms are sometimes present in closely adjacent areas separated by a sharp exposure gradient. For example, the exposed beaches of Barkley Sound, British Columbia (Nudibranch Point and Brady's Beach), are only about 2 km from Banifield Inlet and currents flow freely between the sites. Yet the animals at each site are distinctly different in form. There is no reason to suspect a barrier to larval dispersal, so differences are probably due to ecophenotypic (physiological) adaptation rather than genetic isolation.

Styela montereyensis rarely occurs in quiet water near the southern end of its range (Fay and Vallee, 1979). For example, in Newport Bay, California, where the stalked *Styela clava* has been introduced (Johnson and Abbott, 1972), *Styela montereyensis* is not found, despite the proximity of open water populations from which a bay population could be recruited. *Styela clava* has a ventrally- or anteriorly-directed incurrent siphon and a short stalk; it is almost identical in form to the Neah Bay *Styela montereyensis*. It is not known whether induced flow aids *Styela clava* in feeding or whether intrageneric competition excludes *Styela montereyensis* from Newport Bay.

Previous studies have shown that tadpoles of many ascidian species are photopositive at hatching or upon release from the parent colony, and then develop a strong photonegative response at the time of settling. This results in a preference for cryptic sites. By contrast, *Styela montereyensis* tadpoles in the dark delay metamorphosis for a short time. Beyond this, they are quite non-discriminating with regard to light or substratum. It is reasonable to suppose that photonegative behavior has been selected out of the behavioral repertoire of *Styela* as a maladaptive trait, since cryptic sites are probably the least suitable places for taking advantage of surge currents.

Despite the larvae's apparent non-discrimination, a large percentage of adults are found in unobstructed positions where they can orient freely. When animals die, their stalks often remain intact for a time. We have frequently found more stalks than animals on intertidal vertical surfaces, lending credence to the idea that the observed pattern of distribution results primarily from differential mortality following a nearly-random settlement.

Jorgensen (1955) has pointed out that most filter-feeders must expend a large proportion of their assimilated energy on food collection because of the relatively

low concentration of usable particulate matter suspended in the sea. Because of its induced flow foraging method, *Styela* may be an exception to this generalization. At Neah Bay, animals recruited in the spring of 1979 grew to an average length of 13 cm by November. In Monterey Bay, we have found specimens as long as 32 cm, though Van Name (1945) reported the upper size limit of the species to be 20 cm. *Styela* has a lower basal metabolic rate than congeneric species found in quiet bays (C. Lambert, California State University, Fullerton, personal communication, 1978), and it is capable of spawning viable gametes in every season of the year. We suggest that a low energy demand for food gathering permits low metabolism and also frees energy for large size, indeterminate growth, and continuous reproduction.

Numerous stalked ascidians from the deep sea have recurved incurrent siphons (Van Name, 1945; Kott, 1969; Monniot and Monniot, 1978). Of special interest are species in several families with completely unciliated branchial baskets. The incurrent siphons of these forms are often hypertrophied. Although their modes of particle capture remain a mystery, Kott (1969) and Monniot and Monniot (1978) have independently speculated that bottom currents could greatly enhance their feeding by inducing flow. While *Styela montereyensis*, living in strong surge, has a strong branchial basket with small stigmata, the stigmata of deep sea forms are large, seeming to provide less resistance to the dynamic pressure of even slight currents. The fact that many of these species are found in shallower water only where there are strong upwelling currents (Monniot and Monniot, 1978) supports the hypothesis that they collect food in much the same way as *Styela*.

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SUMMARY

1. Ambient water currents enhance internal flow and feeding in *Styela montereyensis* by forcing water through the branchial basket. Induced flow depends on upstream orientation of the incurrent siphon.

2. In open-coast and protected-outer-coast habitats, most animals occur in surge channels or on upward-facing horizontal surfaces where they sway freely with the surge. Orientation takes place as the flexible stalk bends with the passing of each wave, keeping the posteriorly-recurved incurrent siphon directed upcurrent.

3. In calmer water, animals' growth form is characterized by relatively shorter stalks and ventrally-inclined incurrent siphons. Adults in these habitats are mostly oriented with the mid-sagittal plane parallel to the surface of the water. This orientation allows the ascidians to utilize the dynamic force in water surges coming from a single direction.

4. Observed patterns of microdistribution probably result from differential mortality rather than habitat selection. Larvae delay metamorphosis for a short time in complete darkness and show no strong preferences for shaded substrata. Otherwise, they seem almost non-discriminatory with regard to attachment sites.

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